

shape often highly irregular. Brachial valve vestigial occupying a small posterior triangular area of a large plate of fibrous calcite presumed to have been deposited by an infold of the mantle and to have given support to a ptycholophous or more usually a schizolophous lophophore. Pedicle valve extending posteriorly as an enormous flap intimately connected with the pedicle valve apically and posterolaterally and invariably retroflexed along a narrow median zone lying immediately dorso-posteriorly to the brachial valve, posterior flap highly variable in form, usually the principal organ of fixation and moulded to the base affording anchorage, less frequently strongly retroflexed to come in contact with the external surface of the apical part of the pedicle valve or growing anteriorly and ankylosed to the sides of the pedicle valve to form with it a deep cone. In early stocks the median area of the pedicle valve interior surrounded by a low ridgelike flange indented to form a median loop and a variable number of lateral loops; in later stocks the sides of loops coalesced to form solid septa; internal plate of brachial valve lobated to correspond to the loops or septa. Upper Carboniferous to Permian.

Family OLDHAMINIDAE Schuchert and LeVene, 1929

Oldhaminoids with the loops or septa and hence the lobation of the brachial internal plate

symmetrically disposed about the median line. Upper Carboniferous to Permian. Type genus *Oldhamina* Waagen.

POIKILOSAKIDAE, n. fam.

Oldhaminoids with the loops or septa and corresponding lobes of the brachial internal plate developed in an irregular fashion. Upper Carboniferous to Permian. Type genus *Poikilosakos* Watson.

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ENTOMOLOGY.—*Additional material on the phylogeny and dispersal of Atopsyche (Trichoptera: Rhyacophilidae)*.¹ HERBERT H. ROSS, Illinois Natural History Survey, Urbana, Ill.

The intermingling of elements of South American and North American biotas across the Central American region is a study full of fascination. The fossil record for any terrestrial group in this critical area is very scanty, so that pertinent evidence from biogeography may be our best source of information on certain phases of the subject for some time to come.

Since Dr. King and I prepared our first paper on the dispersal pattern of the genus *Atopsyche*, known only from this area, I have been fortunate in obtaining several additional lots of material and in being

¹ This study was aided by a grant from the John Simon Guggenheim Memorial Foundation.

able to study the type of *A. implexa* (Navas). Although the new material adds only eight species to the 21 previously analyzed, it brings out several points of biogeographic interest. These fit well the concepts and postulates set forth in the earlier paper on the genus (Ross and King, 1952, Ann. Ent. Soc. Amer. **45**: 177-204) extending some ideas and suggesting modifications of others.

In the first place, the new species *ulmeri* from Peru is a close relative of *cira* from Costa Rica and demonstrates a spread of this otherwise northern group from Central America into South America. This was probably a post mid-Pliocene dispersal.

It was originally suggested that at this time two South American lines spread into North America, and we wondered why we had no evidence of a complementary spread of a North American form into South America. Here it is.

Two items concern the *ikonnikovi* complex, here renamed the *kingi* complex. We thought this complex originated in South America in the Miocene, but had no really primitive South American species as evidence. The new species *kingi* from Peru proves to be such a primitive member. In addition, a new subgroup of the *kingi* complex has been discovered, typified by a pair of curious, setose, oval bodies on the third and fourth tergites of the males, fig. 5C. This subgroup contains three known species—a primitive one, *vatucra*, from Peru; a more specialized species, *banksi*, from Colombia; and the hitherto misplaced species *implexa* from Costa Rica. This distribution pattern complements that of the *kingi*, *dampfi*, and *boneti* triad.

A fourth point is the finding of a very primitive member of the *batesi* group in Peru, the new species *alconura*. It was postulated on phylogenetic evidence that this line originated from South American ancestors, although the known members came from Mexico and the West Indies. The discovery of a primitive form, *alconura*, in Peru suggests that the progenitor of the group may have differentiated in South America before dispersing to other areas.

The other two new species involve no controversial points. *A. explanata* from Peru is a close relative of *kamesa*, from Bolivia. *A. serica* from Brazil is the most primitive member yet known of the *longipennis* group, and emphasizes the relationship between the different lines within the group.

Unless otherwise stated, types of the new species are deposited in the collection of the Illinois Natural History Survey.

Subgenus *Atopsyche* Banks

The opportunity to study the type male of *Ventrarma implexa* Navas, the genotype of *Ventrarma* Navas, shows that it is a member of the typical subgenus *Atopsyche* and not a member of the group considered as the distinctive sub-

genus *Ventrarma* by Ross and King, 1952. *Ventrarma* must therefore be placed as a synonym of the subgenus *Atopsyche*. A new name, *Atopsaura*, is proposed later in this paper for the other segregate.

Atopsyche ulmeri, n. sp.

Male.—Length 5.5 mm, front wing 5 mm. Color light brownish yellow with darker areas on the mouthparts, front legs, and thorax; wings variegated with irregular light and medium spots of brown. General structure typical for genus. Abdomen with third tergite bearing a faint basal band of minute setae, fifth sternite with a small dorsal projection near base of segment. Male genitalia as in Fig. 1. Paracercus elongate with a high sharp point in middle, apical portion elongate, narrow, and curved sharply laterad at apex. Filicercus short, with a few setae at or near tip. Clasper very elongate and slender, with apical segment short, hooked at apex, with the ventral margin rounded. Aedeagus short and broad, with a narrow lateral flange.

Holotype.—Male, Paucartambo, Ccosnipata Valley, Cusco, Peru, November 15, 1951, Felix Woytkowski. *Paratypes*.—Same data, but November 26, 1951, 3♂.

This species is most closely related to *cira* (Mosely), differing in the slender apex of the paracercus and the undivided apex of the aedeagus.

Atopsyche explanata, n. sp.

Male.—Length 7.5 mm, front wing, 7 mm. Color yellowish brown below, darker brown above, the wings a light shade of chocolate brown. Abdomen simple, without setal bands on segment three and with only a small process on the fifth sternite. Male genitalia as in Fig. 3. Paracercus slender and elongate, apparently with only the apical point, and bearing at the apex a cluster of long, stout setae. Filicercus of moderate length, with an irregular scattering of setae on the apical half. Clasper with basal segment twice as long as wide, apical segment slightly more than half length of basal one, curved and constricted in middle so as to form a clavate apex and a bulbous base. Aedeagus with a large, high, bilobed central portion, and produced on each side of this into a wide, up-curved flange. In repose the paracercus fits between the flange and the central high portion of the aedeagus.

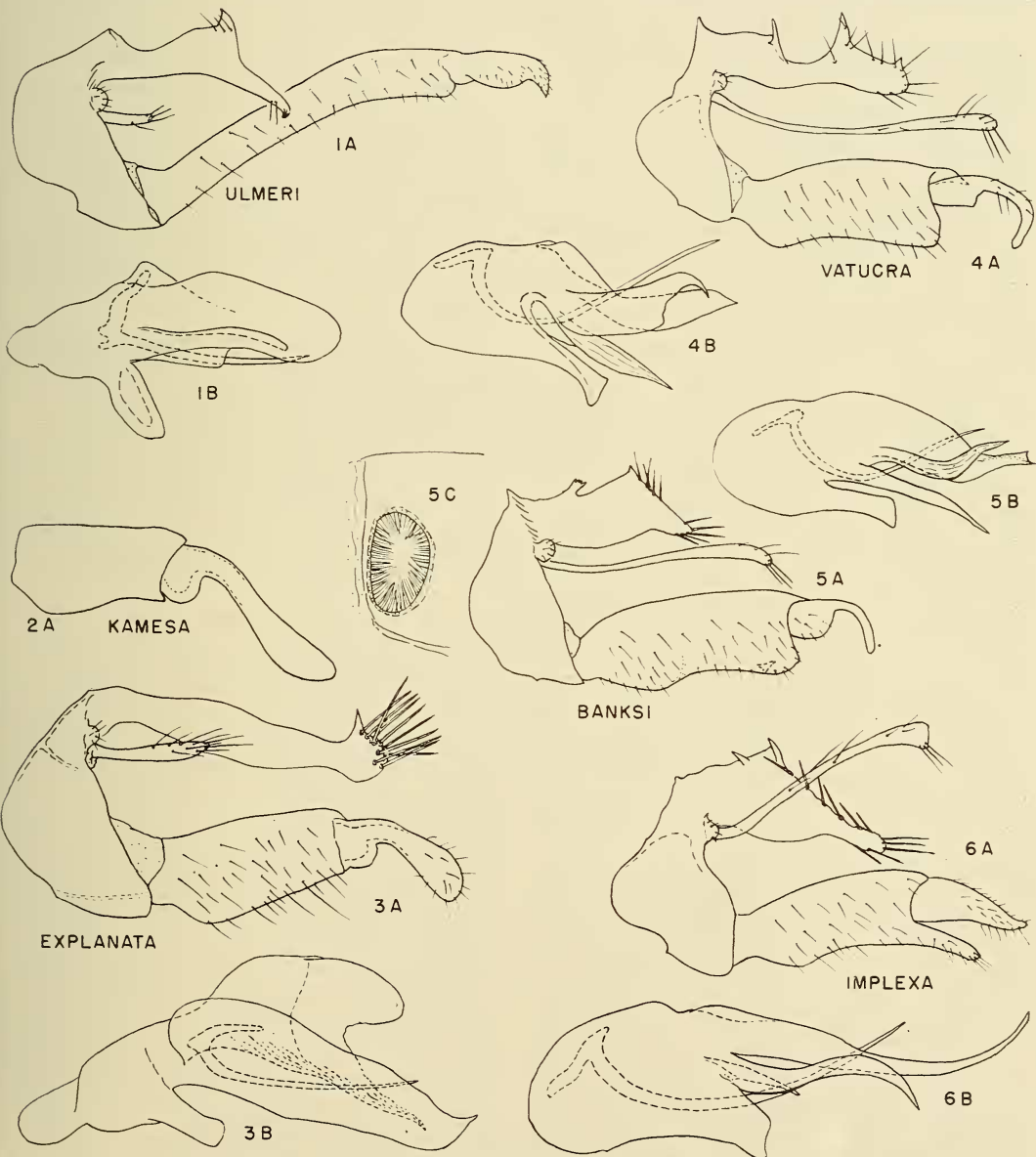
Holotype.—Male, Paucartambo, Ceosnipata Valley, Cusco, Peru, November 17, 1951, Felix Woytkowski.

This species is a close relative of *kamesa* Ross and King, differing in the shorter apical segment of the clasper and the shallower lateral flange of the aedeagus. The true division between the two segments of the clasper is sometimes difficult to see and in the original description of *kamesa* was not truly shown. A corrected drawing

of the clasper of *kamesa* is included here for reference, Fig. 2A.

Atopsyche kingi, n. sp.

Male.—Size and color almost identical with the preceding except that the color is slightly darker and the tibiae and tarsae are covered with brownish hair. Abdomen with third tergite bearing an irregular, somewhat oval, corner patch of minute hairs on anterolateral angle;



Figs. 1-6.—Male genitalia and associated structures of *Atopsyche*: A, Genital capsule, lateral aspect; B, aedeagus, lateral aspect; C, oval body on fourth abdominal tergite.

this same corner of the segment on the third and fourth tergites is produced into a short internal sclerotized band ending in a broader, rounded apex, Fig. 7*F*. Fifth sternite with only a short process. Genitalia as in Fig. 7. Paracercus with a high middle projection and a lower point at apex. Filicercus elongate and clavate. Clasper with basal segment moderately long and stout, with a somewhat angulate mesal shoulder near middle; apical segment short, broad, and curved ventrad at tip. Aedeagus with apical portion divided into two pairs of processes, the ventral pair shorter and dark, the dorsal pair longer and asymmetrical.

Holotype.—Male, Paucartambo, Ccosnipata Valley, Cusco, Peru, November 27, 1951, Felix Woytkowski. *Paratypes*.—Same data, including dates November 20, 26, and 27, 17♂.

This species is a primitive member of the *kingi* complex differing from the other members of the complex in lacking the basal tooth on the paracercus and from other species of the genus in the elongate pair of processes on the aedeagus.

The internal straplike appendage at the base of the third and fourth tergites is a most useful character in this complex. It occurs in all the members of the *kingi* complex which are available for study. In these complexes also the internal rod appears to have moved from the ventral end of the basal angulation to the dorsal end, and the apex of the aedeagus is divided into several foliatus lobes. These are at variance with the available description of *ikonnikovi*, in which the internal rod of the aedeagus is illustrated as being attached at the ventral end of its basal angulation, and the apex of the aedeagus is simple as in the *bolivari* complex. For this reason the exact placement of *ikonnikovi* is open to question. If it is indeed related to *kingi* and its relatives, then *ikonnikovi* would seem to be a more primitive member of the same line. On the other hand the two pre-apical processes on the paracercus are most unusual in that the basal one is the larger instead of being the smaller as in members of the *kingi* complex. Until actual material is available for study, *ikonnikovi* can be placed only tentatively, and perhaps best at the base of the *kingi* line. Under these conditions it seems better to use a new complex name for the aggregation of species *boneti*, *dampfi*, *kingi* and the three following, and I am using

the term *kingi* complex, naming it after the most primitive known member.

Atopsyche vatucra, n. sp.

Male.—Length 6.5 mm, front wing, 6 mm. Color identical with the preceding, being a moderately dark brown for the genus. Abdomen with tergite three and four each bearing a curious oval body, Fig. 5*C*, on the antero-lateral corner of the tergite, and also the internal spatulate strap as in Fig. 7*F*; process of fifth sternite small. Genitalia as in Fig. 4. Paracercus with three points, the middle one large and high, the basal one smaller and spur-like, the apical one small. Filicercus elongate and slightly clavate. Basal segment of clasper almost rectangular, the ventral margin slightly incised and the apico-dorsal corner slightly produced on the mesal side; apical segment with the apical portion slender, finger-like and hooked. Aedeagus with three pairs of lateral processes as shown in Fig. 4*B*.

Holotype.—Male, Paucartambo, Ccosnipata Valley, Cusco, Peru, November 26, 1951, Felix Woytkowski. *Paratypes*.—Same data, 2♂.

This and the following two species form a distinct subgroup of the *kingi* complex in which the third and fourth abdominal tergites have the odd oval bodies shown in Fig. 5*C*. Of the three, *vatucra* is the most primitive as shown by the three distinct points on the paracercus.

Atopsyche banksi, n. sp.

Male.—Length 10 mm, front wing 9.5 mm. Color fairly dark brown with the usual mottling of various colored hair on the front wings. Abdomen with structures of the third and fourth tergites and fifth sternite identical with the preceding. Genitalia as in Fig. 5. Paracercus triangular, the apical point not evident, the middle point small but on a high triangular crest, the basal point short and stubby, its tip divided into several minute points. Filicercus elongate and clavate. Clasper with basal segment somewhat rectangular, the ventral margin slightly incised, and bearing a short mesal pointed projection near apex and a broad shoulder near base; apical segment with basal portion round, apical portion narrow, fingerlike, and curved sharply ventrad. Aedeagus with apical portion divided into three pairs of lateral lobes shaped as shown in Fig. 5*B*.

Holotype.—Male, San Antonio, Colombia,

1,800 meters elevation, February, Fassl. coll. (Museum of Comparative Zoology).

This species is a close relative of *vatucra*, the two being obviously grouped together on the basis of the odd clasper. From *vatucra*, *banksi* differs in the shape of the point on the paracercus and the lobes of the aedeagus.

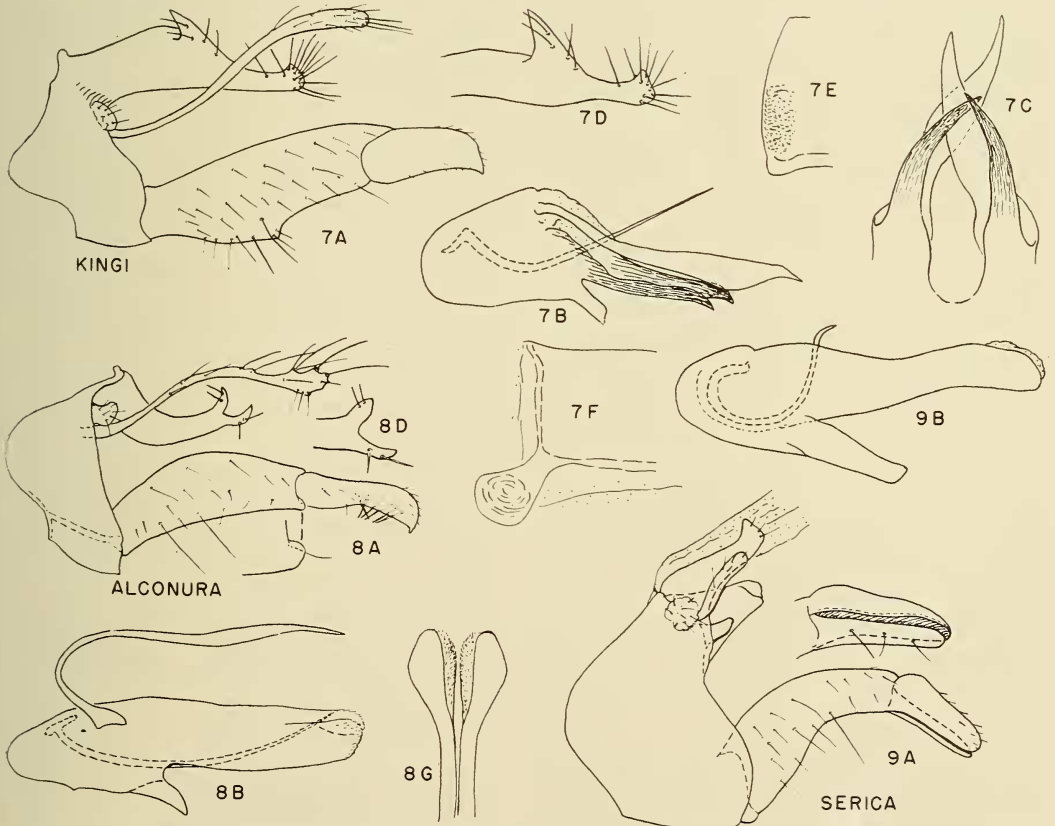
Atopsyche implexa (Navas)

Thanks to the courtesy of officials of the Paris Museum, the type male of this species was studied in detail and compared with a second specimen, also labeled "Costa Rica" which was identical with the type and was made available for further study. To supplement the original description the following is added, together with illustrations of parts in Fig. 6.

Male.—Length 8 mm, front wing 7.5 mm. Structures of abdominal tergites three and four and sternite five, identical with those of the preceding two species. Male genitalia as in Fig.

6. Paracercus high and trianguloid, with no apical point but with middle and basal points spurlike. Filicercus elongate and almost clavate at apex. Clasper fairly broad, with apico-ventral corner produced into a long fingerlike projection which extends two thirds along the apical segment; apical segment almost triangular but also sinuate, tapering to a sharp point. Aedeagus with three pairs of lateral processes, the upper pair very long, the middle pair fairly long, and the ventromesal pair very short and scarcely visible from lateral view.

The resemblance of the clasper to that of *majada* is quite striking, and on this evidence alone the species was originally considered a possible close relative of *majada*. Details of abdominal tergites three and four, of the various structures of the aedeagus, and the paracercus, however, demonstrate clearly that this species is not at all close to *majada* but instead belongs in the *kingi* complex.



FIGS. 7-9.—Male genitalia and associated structures of *Atopsyche*: A, Genital capsule, lateral aspect; B, aedeagus, lateral aspect; C, apex of aedeagus, ventral aspect; D, apical portion of paracercus, ventrolateral aspect; E, anteroventral corner patch on fourth abdominal tergite; F, inner view of opposite anterior corner showing spatulate process; G, apex of aedeagus, dorsal aspect.

To date this species is known only from the type, bearing the data "La Caja, Costa Rica, Paul Serre 1920," and specimen here studied, labeled "Costa Rica."

Atopsyche dampfi Ross and King

Previously known only from Mexico, a record for another country may be added: Rosario Mines, Honduras, April 30, M. Bates, 1 male. (Museum of Comparative Zoology)

Subgenus *Atopsaura*, n. subgen.

As explained earlier, the genotype of *Ventrarma* actually does not apply to the group which was called the subgenus *Ventrarma* by Ross and King. For this latter segregate I am proposing the name *Atopsaura*. The genotype is hereby designated as *Atopsyche hamata* Ross and King.

Atopsychealconura, n. sp.

Male.—Length 6.5 mm, front wing 6 mm. Color fairly light brown, intermediate between the yellowish brown of *ulmeri* and the darker brown of the other species. Abdomen with tergite three having a very faint basal band of minute hairs, and with process of fifth sternite small. Genitalia as in Fig. 8. Paracercus elongate and curved dorsad, the apex divided into two sharp processes, with no projections basad of these. Filicercus elongate; its apex is almost capitate, and is irregular due to the wartiness of the bases of the setae. Clasper with basal segment somewhat bowed, its apico-ventral corner slightly produced into a rounded extension overlapping the corner of the apical segment, apical segment moderately slender, largest in middle, the extreme apex produced into a short ventral point, and the mesal margin armed with several long sharp setae. Aedeagus simple, except for the dorsal spine typical of the *batesi* group.

Holotype.—Male, Paucartambo, Ccosnipata Valley, Cusco, Peru, November 26, 1951, Felix Woytkowski. *Paratype*.—Same data, 1♂; Canggallo, south Peru, 2,600 meters elevation, 1♂ (Hamburg Museum).

Judged by the short apicoventral process of the basal segment of the clasper, this species seems to be the most primitive known member of the *batesi* group. It is readily distinguished from the other members by this character and by the curious bifurcate tip of the paracercus.

Atopsyche serica, n. sp.

Male.—Length 8.5 mm, front wing 8 mm. Color dark brown with the usual mottling. Abdomen without special structures on the third and fourth tergites and with only a small process on the fifth sternite. Genitalia as in Fig. 9. Paracercus very short, directed more dorsad than posteriad, and with neither middle nor basal point. Filicercus slightly shorter, fingerlike. Ventrad and mesad of these two structures is a short thumblike projection. Between the filicerci and below the tenth tergite is a curious horse-shoe-shaped structure beneath which the aedeagus protrudes. In lateral view this appears as an inconspicuous hoodlike structure between the paracerci. Basal segment of clasper bowed and directed more dorsad than usual; its ventral mesal margin is apparently produced into a long, narrow flange which extends along the inner side of the apical segment, which is grooved to receive it; apical segment elongate, oval, widest near base, and rounded at apex. Aedeagus very simple, the internal rod coiled as in *longipennis*.

Holotype.—Male, Nova Teutonia, Brazil (27°11' B, 52°23' L) October 4, 1939, Fritz Plaumann (Museum of Comparative Zoology).

This species is closest to *longipennis* but the claspers are a little more suggestive of *hamata*. It is distinguished from all other members of the group by the extra pair of short lateral processes below the filicercus and the sclerotization of the structure above the opening for the aedeagus.

This species emphasizes the unusually rapid rate of morphological differentiation which has occurred between species of the *longipennis* group in contrast with the species of other groups in the genus. It is also interesting to note that in this species unusual pairs of processes have been added which are reminiscent in both position and appearance of structures in some of the Australian and New Zealand genera which are only distantly related to *Atopsyche*. This demonstrates the tendency toward the parallel development of similar genitalic structures in the tribe.

Atopsyche falina Ross and King

An additional record has been received from Argentina, the only country for which this species is known: El Tuncho Catanarea, Argentina, 2500 meters elevation, May 5, Jorgansen, 2♂ (Museum of Comparative Zoology).

Atopsyche mexicana (Banks), n. comb.

Philopotamus mexicanus Banks, Trans. Amer. Ent. Soc. 27: 370. 1901.

The type, in the Museum of Comparative Zoology, was examined in 1951 and found to be without abdomen, so that it is not possible at present to identify the specimen beyond genus.

The venation indicates definitely that it belongs to *Atopsyche*.

Atopsyche callosa (Navas)

I had an opportunity to study the type in the Paris Museum. Although labeled and recorded in the original description as a male, the specimen actually is a female, and could not be identified except to genus.

ORNITHOLOGY.—*Feeding adaptations and systematics in the avian order Piciformes*. WILLIAM J. BEECHER, Chicago Natural History Museum. (Communicated by Herbert Friedmann.)

Recently Dr. Herbert Friedmann offered for my study some spirit specimens of honeyguides (Indicatoridae), together with other members of the order Piciformes. It was hoped that such an investigation as I carried out for the Neotropical honeycreepers (Beecher, 1952) might cast further light on both the feeding adaptation and systematic position of these birds so well studied by Friedmann (in MS.). Checking the systematic position of the honeyguides required a somewhat hasty completion of a long-time survey of jaw musculature in the class Aves which I will publish elsewhere. The present paper simply deals with the food adaptations in the head region of the piciform honeyguides, barbets, puffbirds, jacamars, toucans, and woodpeckers, which seem to occupy an interesting position between the perching birds (Passeriformes) and the remaining avian orders. Specimens used are from the collections of the United States National Museum and Chicago Natural History Museum. For their use or for advice, I am indebted to Herbert Friedmann, Austin L. Rand, Emmet R. Blake, and D. Dwight Davis.

SPECIMENS EXAMINED

Although a limited number of anatomical specimens was studied, the use of numerous skulls of related species considerably swells the list of material examined. This material is sufficient to suggest very strongly that the same constancy of muscle pattern found to hold for the species of passerine families holds for non-passerine families as well. Species dissected are: (Indicatoridae) *Indicator minor conirostris*, *I. exilis*, *I. maculatus*,

I. minor minor; (Ramphastidae) *Pteroglossus torquatus*, *Ramphastos cuvieri*, *Selenidera spectabilis*; (Capitonidae) *Lybius leucocephalus*, *Megalaema haemacephala*, *M. rafflesii*, *M. zeylanica*, *Trachyphonus purpuratus*; (Bucconidae) *Chelidoptera tenebrosa*; (Picidae) *Colaptes auratus*, *Dryocopus pubescens*, *Melanerpes carolinus*, *M. erythrocephalus*, *Piculus chrysochloros*, *Picumnus squamulatus*. No specimens of jacamars were on hand to dissect, unfortunately, but skulls strongly suggest their close alliance with the barbets.

INVESTIGATION TECHNIQUES

In undertaking this study I have pursued essentially the plan laid out in my paper mentioned above and in the more comprehensive work on the phylogeny of the Oscines (Beecher, 1953). This consists in comparing various systems throughout the groups considered, as illustrated in the figures for the families. In each of these the jaw musculature is illustrated in side view and oblique view (with eye removed), as indicated in black on the accompanying skull drawings. The tongue is drawn on the right above and the ectethmoid plate with its foramina (separating the orbital and nasal cavities), on the left. In the center is figured the horny palate pattern and the bill. The logic behind the comparison of systems is that it should be possible in an avian order to establish a ground plan from which the groups (families) are adaptively specialized. Special emphasis was placed on jaw muscle pattern as a family trait in the Oscines because song-bird families appear to be diverging from such a ground plan under the selection pressure of different food types and because each family tends to have a very constant pattern. In the present